

IS TIBETAN POLYANDRY ADAPTIVE?

Methodological and Metatheoretical Analyses

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This paper addresses methodological and metatheoretical aspects of the ongoing debate over the adaptive significance of Tibetan polyandry. Methodological contributions include a means of estimating relatedness of fraternal co-husbands given multigenerational polyandry, and use of Hamilton's rule and a member-joiner model to specify how inclusive fitness gains of co-husbands may vary according to seniority, opportunity costs, and group size. These methods are applied to various data sets, particularly that of Crook and Crook (1988). The metatheoretical discussion pivots on the critique by evolutionary psychologists of adaptationist accounts of polyandry. Contrary to this critique, I argue that valid adaptationist explanations of such practices do not necessitate cognitive mechanisms evolved specifically to produce polyandry, nor that there must have been exact equivalents of Tibetan agricultural estates and social institutions in human evolutionary history. Specific issues raised when one posits either kin selection or cultural evolution to explain the adaptive features of Tibetan polyandry are also discussed.

KEY WORDS: Evolutionary psychology; Inclusive fitness; Kin selection; Mating systems; Member-joiner conflicts; Optimal group size; Polyandry; Tibet.

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The title of this paper refers to two controversies in the study of human behavioral adaptation. One is empirically specific and concerns whether the practice of fraternal polyandry—rare among humans but fairly common among certain groups of ethnically Tibetan agropastoralists—produces a net gain in the calculus of inclusive fitness. The other controversy involves a metatheoretical dispute about the proper scope and form of questions we should ask about the adaptiveness of human behavior—a dispute sometimes glossed as “Darwinian psychology vs. Darwinian anthropology” (Symons 1989). These two seemingly disparate issues are linked because the most empirically detailed adaptationist study of Tibetan polyandry published to date (Crook and Crook 1988) has been singled out as a prime example of the sort of analysis that, in Symons’s (1989:139) words, “contains not a single well formed description of a Darwinian adaptation” and therefore “implies nothing about the evolution of phenotypic design.” The present paper is framed in this dual context, thus tackling a set of specific methodological and conceptual problems involving a particular institution (fraternal polyandry) in a specific set of populations (ethnic Tibetans) while also addressing a more general set of issues concerning the study of human adaptation.

The first issue—is Tibetan polyandry adaptive?—is examined in terms of two more specific questions: (1) What is the best method to use in calculating inclusive fitness gains? (2) Adaptive for whom? The answer to the first involves an exploration of the logic of Hamilton’s rule (Hamilton 1963, 1975) and certain genealogical technicalities, but it also necessarily intersects with the answer to the second question. That is because the inclusive fitness effects of polyandry are likely to vary by birth order (senior vs. junior brothers), generational status (parent vs. offspring), sex (male vs. female), and opportunity costs (i.e., the alternatives to polyandry, and their payoffs).

The second debate—is Tibetan polyandry an adaptation?—turns on other issues, including: (1) How specific and evolutionarily novel are the conditions favoring polyandry? (2) How specialized are the evolved psychological mechanisms underpinning adaptive behavior? (3) If polyandry is ascribed to kin selection, what does this imply for the inheritance mechanism? (4) If polyandry is a product of cultural evolution, what does this imply for the adaptive outcome?

INCLUSIVE FITNESS: METHODOLOGICAL ISSUES

The Crook and Crook (1988) study provides the most detailed attempt yet published to evaluate the inclusive fitness of polyandry. Not incidentally,

it also provides the only set of published data complete enough to perform such an evaluation. The paper contains data on completed family size for 29 Tibetan estate families near Leh village, Zangskar district, Ladakh (a subregion of ethnic Tibet within the political boundaries of India). Of these families, 10 had polyandrous marriages with 2 to 4 co-husbands. The 19 monogamous unions are in turn divided into those of estate heirs (*khang.chen* or “main house” families), totaling 12 cases, and those of junior brothers who violate the monomartial principle of one marriage per set of brothers and occupy a position of lesser status and a minor dwelling (*khang.chun*), the remaining 7 cases. The key data are given in Crook and Crook’s Table 5.3, reproduced here in simplified form (Table 1). Note that non-heirs have lower reproductive success than monogamous heirs (2.0 vs. 3.75), and that polyandrous unions produce more offspring on average than monogamous ones, even within estate marriages (5.19 vs. 3.75).¹

It is perhaps no surprise that minor marriages (monogamous marriages by junior brothers which establish separate *khang.chun* households), with their scarcer material and human resources, produce fewer surviving offspring. The more interesting question is, do brothers jointly inheriting an estate and cohabiting in fraternal polyandrous marriages suffer a reduction in inclusive fitness? To answer this question, Crook and Crook derive an equation for comparing the inclusive fitness yields of polyandry vs. monogamy. They employ this equation to calculate the family sizes that are needed to give a senior brother sharing his spouse with one or more fraternal co-husbands inclusive fitness equal to that he would enjoy as sole estate heir—what I term the “isofitness” values for various degrees of polyandry. Using the Crook and Crook equation and their Zangskar data yields an isofitness threshold of 5.0 offspring for diandry (two co-husbands) (Table 2); below this, the senior brother is making a sacrifice in inclusive fitness by sharing his wife and estate with a younger brother.² Significantly, this value is slightly higher than that actually averaged in the six documented diandrous unions (Table 1).

There are some ambiguities in this result, however. First, the Crook and Crook (1988) analysis assumes that co-husbands are full sibs, thus em-

Table 1. Completed Family Size and Marriage Type on Zangskar Estates (after Crook and Crook 1988:Table 5.3)

Non-heir (<i>khang.chun</i>) families	Estate-heir (<i>khang.chen</i>) families			
	Monogamous	Diandrous	Triandrous	Tetrandrous
2.0 (n = 7)	3.75 (n = 12)	4.8 (n = 6)	4.7 (n = 3)	9.0 (n = 1)

Table 2. Isofitness Family Sizes for Estate Monogamy vs. Diandry (Zangskar)

Marriage type (number of co-husbands)	Crook and Crook formula ^a	Revised <i>r</i> value ^b	Revised <i>e</i> value ^c	Observed offspring ^d
Estate monogamy (1)	—	—	—	3.75
Diandry (2)	5.0	5.1	5.5	4.8

^aThe values obtained by employing their formula (Crook and Crook 1988:108), which are slightly different than stated in their text (1988:109).

^bEmploys the revised equilibrium value of $r = 0.465$ derived for multigenerational polyandry (see text).

^cUnlike previous calculations, this one assumes that brothers not joining estate marriages will average 0.54 offspring (see text).

^dThe mean number of offspring reported in Crook and Crook (1988: Table 5.3).

ploying a coefficient of relatedness of 0.5. But in the case of recurrent polyandry, co-husbands are themselves likely to be products of a polyandrous union, and if so their coefficient of relatedness will necessarily be less than that of full-sibs (but more than that of half-sibs who have one unrelated parent).³ What effect might this have on the inclusive fitness calculations proposed by Crook and Crook?

To find out, we first have to determine the equilibrium value that r , the coefficient of relatedness, will reach in a system of recurrent polyandry. According to a derivation performed by Alan Rogers (see Appendix), the value of r between children descended from a line of polyandrous unions will stabilize at

$$r = (h + 1) / (3h + 1) \quad (1)$$

where h is the number of co-husbands. If h varies from family to family and generation to generation, then as Rogers points out (see Appendix) one should employ its harmonic mean H , where

$$H = n / \sum(1/h) \quad (2)$$

for n conjugal units. Using this formula, and the frequency distribution of co-husbands in 22 estate marriages given by Crook and Crook (1988:Table 5.3), we can calculate H to be 1.354 (as compared to the arithmetic mean of 1.68). This yields an expected value of r between co-husbands of 0.465. Although based on a small sample of marriages, these figures are remarkably close to comparable data from three other studies of ethnic Tibetans in other locales, each with larger samples (see Table 3).⁴

As expected, this value of r is lower than the full-sib case. If we employ it to calculate inclusive fitness returns from polyandrous marriage, the fitness realized through co-husbands' offspring is reduced by about 7%, all else being equal.⁵ The resultant isofitness value for a diandrous union rises slightly (Table 2), making polyandry even less profitable in inclusive-fitness terms.

Table 3. Comparative Data and Estimates of h and r

Group (Source)	Mean number of co-husbands ^a			Estimated coefficient of relatedness ^b
	Arithmetic	Harmonic	Polyandrous	
Zangskar (Crook and Crook 1988)	1.68	1.35	2.50	0.465
Nyinba (Levine 1988, 1983 census)	1.68	1.48	3.23	0.456
Chimbro (Goldstein 1971)	1.68	1.41	2.28	0.461
Limi (Goldstein 1976)	1.71	n.d.	2.70	n.d.

^aArithmetic mean = (total married men / total number of marriages); harmonic mean as defined in equation 2; polyandrous mean = (total polyandrously married men / total number of polyandrous marriages). All figures newly calculated using data in sources indicated.

^bCalculated according to equation 1, using the harmonic mean of h . (See text, note 4 for discussion of methodology and sources.)

A second ambiguity arises from the fact that Crook and Crook assume that junior brothers will produce no offspring at all if they are not included in the main estate marriage. However, their own data indicate an average value of 2.0 offspring for 7 minor marriages (see Table 1); they also note that 30% of brothers in the study area were (presumably celibate) monks (1988:104). If we take these two facts as the basis for estimating the reproductive success of brothers not included in polyandrous estate marriages, the resultant value is 0.54 expected offspring.⁶ Again, this has the effect of lowering the fitness returns from polyandry relative to monogamy (Table 2).

Finally, all of the above calculations refer to an individual who could expect to average nearly 4 (i.e., 3.75) offspring as monogamous heir to an estate. Yet only one brother in a given cohort of sibs—generally the senior one—can experience this result. The remaining brothers (if any) must choose between polyandry and some reproductively less rewarding option (as noted below). These considerations suggest that the analysis of polyandry requires a framework that takes the differing interests and opportunity costs of the various players more fully into account.⁷ The following section is devoted to that task.

ADAPTIVE FOR WHOM? POLYANDRY AS A MEMBER-JOINER GAME

There are in fact several categories of actors in the cultural complex of Tibetan polyandry, each with overlapping but distinct interests: junior and senior brothers, their sisters, the women who marry them, and the

parents of each of them. Since the focus here is on marital decisions within the brothers' family, I will not consider women's interests and outcomes or those of their parents, though this is an interesting and perhaps understudied topic.⁸ Instead, I will focus on brothers (potential co-husbands) and their parents.

In asking what each brother will gain or lose from polyandry, we must consider their other options, or what an economist would call "opportunity costs." Following Crook and Crook (1988), I assume here that the elder brother in any sibship will be favored to inherit the estate should the monogamy option be chosen. Hence the opportunity cost of polyandry for the senior brother is the 3.75 offspring he could expect to father on average if his brothers are not included in the estate (*khang.chen*) marriage. On the other hand, junior brothers who do not join the *khang.chen* monogamous marriages (Crook and Crook 1988:Table 5.3), they might marry into another estate (i.e., uxori locally, what Tibetans term *mag.pa* marriage), or they might become landless laborers (married or unmarried) or celibate Buddhist monks. Based on the available demographic information, I estimate the opportunity cost for junior brothers (the expected number of children they would sire were they not to marry polyandrously) to be 0.54 offspring (see note 6).

Since polyandrous marriage and estate inheritance involve cooperation between individuals with differing opportunity costs, the optimal choice depends on the available options. This in turn depends in part on one's seniority in the sibship: the eldest son is almost certain to inherit the estate and take a wife, while his younger brothers are only potential members of this conjugal and corporate unit. Viewed this way, Tibetan marital decisions can be analyzed as a member-joiner game, using the model developed elsewhere for foraging group size (Smith 1983, 1985). In such a framework, the choices are not simply between monogamy or polyandry, but between various kinds of polyandry (diandry, triandry, etc.), to the extent that sibship size and composition present these options.

Let us suppose that genetic or cultural evolution has designed men to prefer marital arrangements that on average increase inclusive fitness. Hamilton's rule (Hamilton 1963, 1975; Grafen 1984) proposes that selection favors the propensity to engage in a given type of social interaction only if the effect on the actor's individual fitness plus the effect on the other's individual fitness, devalued by r (the interactors' coefficient of relationship), is positive. Thus, Hamilton's rule states that a net gain in inclusive fitness occurs if (effect on self) + r (effect on kin) > 0. In the present context, the effect on self is the increase or decrease in reproductive success (RS) a man will experience if he or his brother is included in an estate marriage, and the effect on kin is the change in RS the other

brother will experience from the polyandrous arrangement. The analysis that follows (including the generalization to n brothers) is framed accordingly.

In the simplest case of two brothers, the senior brother can expect m offspring if he marries monogamously, while his younger brother will average e offspring if he is excluded from the estate marriage. If the two brothers share a wife and jointly inherit the estate, they will jointly father p offspring. Assuming that polyandrous co-husbands have equal expected paternity, the optimal preference rule for a member (senior brother) is then to include his younger brother as co-husband as long as

$$\frac{1}{2}(p + rp) > m + re \quad (3)$$

while for a joiner (junior brother) the optimal preference rule is

$$\frac{1}{2}(p + rp) > e + rm \quad (4)$$

where r is the coefficient of relatedness between the two brothers (as defined in eq. 2).

To specify a more general framework for any number of brothers, we need two additional variables: n for the total number of brothers in a sibship, and h for the number who are co-husbands ($n \geq h$). The accounting logic is the same, but the algebra is messier. The member's rule is now

$$\left(\frac{p_h}{h}\right) + \left[\frac{rp_h}{h}(h-1)\right] + re(n-h) > \left[\frac{p_{h-1}}{(h-1)} + \frac{rp_{h-1}}{(h-1)}\right](h-2) + re(n-h+1) \quad (5)$$

To unpack this inequality, note that the set of terms on the left-hand side index the fitness gains to Ego if the h^{th} brother is included as a co-husband, while the corresponding terms on the right-hand side are Ego's fitness gains if this brother is excluded (and the marriage thus limited to $h-1$ co-husbands). From left to right, these terms define:

1. the expected number of children fathered by Ego (if the h^{th} brother is included as a co-husband in the estate marriage);
2. the expected number of children fathered by the $(h-1)$ co-husbands, devalued by r ;
3. the expected number of children fathered by the $(n-h)$ brothers who are excluded from the estate marriage and marry monogamously in non-estate marriages or remain bachelors, also devalued by r ;

and on the right-hand side:

4. the expected number of Ego's children if the h^{th} brother is excluded;
5. the expected number of children fathered by $(h-2)$ co-husbands, devalued by r ;

6. the expected number of children fathered by $(n - h + 1)$ brothers who marry monogamously in non-estate marriages or remain bachelors, devalued by r .

The joiner's rule for brothers who are not yet part of a polyandrous estate marriage is similar to equation 5:

$$(p_h / h) + [(rp_h / h)(h - 1)] + re(n - h) > e + rp_{h-1} + re(n - h) \quad (6)$$

As in equation 5, the three terms on each side of inequality 6 correspond to fitness realized through Ego's reproduction, through polyandrously married brothers, and through monogamously married brothers, respectively. In fact, the left-hand side of equation 6 is identical to that of 5, though referring here to a joiner's fitness.⁹

Note that the inequalities above (as well as the formulations given by Crook and Crook 1988) assume that the co-husbands in a polyandrous marriage have equal probability of paternity; that is why Ego's own reproduction in such a union is represented simply as the number of children (p) divided by the number of co-husbands (h). If this is unrealistic (as Crook and Crook in fact suggest it is), then a more complicated formulation with unequal shares will be needed, a point to which I return below.

To apply the member/joiner framework to the Zangskar case, we need estimates of the five variables. Lacking more specific information, I use the data provided by Crook and Crook (see Table 1 in this paper) and equations 1 and 2 to calculate the geometric mean number of co-husbands ($H = 1.354$) and the average relatedness of brothers in a sib cohort ($r = 0.465$); estimate that $e = 0.54$ as explained above; and assume that $m = 3.75$ while p varies with h . Using these values, equations 5 and 6 yield the results given in Table 4.

For "members" (senior brothers considering whether to share estate and wife with a junior brother), polyandry results in reduced inclusive fitness compared with the alternative (estate monogamy where $h = 2$, estate polyandry of $h - 1$ co-husbands where $h > 2$) in all cases except tetrandry. (This last exception is a fragile one, since the single case of tetrandry has an unexpectedly high family size, nearly twice the mean of the three cases of triandry.) On average, members of polyandrous unions lose one-third of an "offspring equivalent" for each additional co-husband included in the estate.

For "joiners" (junior brothers), the situation is reversed: if exclusion means an average RS of 0.54, then joining a polyandrous estate marriage is an inclusive fitness gain at all sizes of h , and it yields an average inclusive fitness dividend of about one offspring equivalent. Thus, the present analysis suggests that polyandry imposes a reproductive cost on

Table 4. Application of Hamilton's Rule to Zangskar Data

Marriage type (number of co-husbands)	Fitness effect if h^{th} brother included ^a		
	Member ^b	Joiner ^c	Grandparent ^d
Diandry (2)	-0.5	1.2	0.5
Triandry (3)	-0.7	0.3	-0.1
Tetrandry (4)	2.1	2.7	4.3
Weighted mean (2.5)	-0.3	1.1	0.7

^aInclusive fitness effect on indicated party if h^{th} brother joins polyandrous union.

^bEffect on a senior brother already inheriting estate, calculated from equation 5.

^cEffect on a junior brother if included in estate marriage, calculated from equation 6.

^dNet effect on number of grandchildren produced by a cohort of sons.

senior brothers and a reproductive gain on junior ones. This directly contradicts the ethnographic observations indicating that senior brothers generally encourage their junior brothers to join the estate marriage, while cases of estate partitioning are generally instigated by junior brothers (Levine and Silk 1997; Kimber Haddix, University of California at Davis, personal communication 1997).

Two factors may account for this contradiction. First, senior co-husbands are likely to father more offspring than junior ones, for a variety of reasons; this could potentially equalize the fitness effects of polyandry, making it fitness-enhancing for all co-husbands (if we take as a given that exclusion can only befall junior brothers).¹⁰ Indeed, Levine and Silk's (1997) analysis indicates that those junior brothers who partition are precisely those most likely to have fewer than expected offspring (given number of years of marriage). Second, the calculated fitness loss to members is on average less than the calculated gain to joiners (Table 4), which suggests the overall fitness gain to any sib cohort would be positive; manipulation by the parents of this cohort to enjoin polyandrous unions would then be reproductively advantageous.

This last idea can be explored further with the Zangskar data. Suppose we ask what marital arrangements would maximize the total number of children produced by a cohort of brothers. For a cohort of two sons, the choice is then between diandry or estate monogamy for the senior son plus exclusion (monkhood, uxorilocal marriage, etc.) for the junior son; for a cohort of three sons, the choices include estate monogamy, diandry, or triandry; and so on. The ethnographic data suggest that this may be a reasonable caricature of the decision framework for Tibetan polyandry. According to Crook and Crook (1988), until recently decisions about polyandry (including how many and which brothers married) were made primarily by the *pha.spun*, composed of the family heads of a group of patrilineally related families. While modeling such a system is beyond the

scope of this paper, we can ask the simpler question: Is polyandry adaptive for the parents of the co-husbands?

Assuming that (grand)parents are related equally to the (grand)children their sons produce in polyandrous and monogamous families we do not need to worry about coefficients of relatedness and can simply compare numbers of surviving offspring. Given the family sizes from Table 1, it is easy to calculate such numbers for h brothers, with either all being co-husbands or $h - 1$ being co-husbands and 1 being excluded from estate marriage. The results (Figure 1) suggest that having as many as four sons marry polyandrously does yield higher fitness payoffs to these men's parents than would obtain if one less son were included in the estate marriage. Thus, if e (the expected offspring production of excluded brothers) is low enough (i.e., ≤ 1.0 in the Zangskar case, well above the estimated value of $e = 0.54$), then moderate levels of polyandry would seem to maximize lineage reproduction.

To return to the kind of analysis employed earlier in this paper, and following the example of Crook and Crook (1988), we might ask what the "isofitness" values might be for polyandry—in other words, how many offspring total would h polyandrously married brothers have to produce to achieve the same inclusive fitness returns as they would achieve if they excluded one brother from the estate marriage? And in turn, how small would the expected RS of brothers who do not participate in polyandry have to be to make adding the h^{th} brother to the polyandrous estate marriage fitness-enhancing? Given the differing interests of various types of individuals, these two questions should be posed separately for "members" and "joiners" in a sib cohort, and for grandparents as well.

The justification for the isofitness analysis has to do with the pitfalls of posing counterfactual questions. The analysis so far has adopted the simplifying assumption that observed demographic outcomes would continue to hold if various alternative pathways had been taken—for example that if any of the polyandrously married men had in fact been excluded from the conjugal unit, then they could expect to produce $e = 0.54$ offspring. But in reality what behavioral ecologists term "phenotypic correlation" is likely to be present; for example, very productive estates may be more likely to produce larger cohorts of sons, who in turn may be more likely to become co-husbands in the next generation's estate marriage. Thus, an isofitness measure provides one sort of sensitivity analysis showing how far one could deviate from the present demographic estimates without altering the sign (positive or negative) of fitness payoff from various conjugal alternatives.

The results of the isofitness analysis are given in Table 5, along with the observed family sizes reported by Crook and Crook (1988). For "members" (more senior co-husbands), polyandry would have to yield about

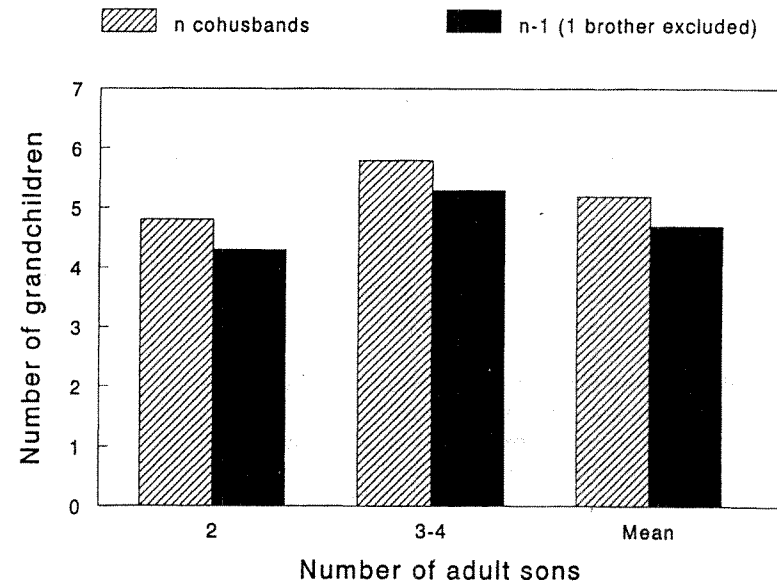


Figure 1. Offspring (grandchildren) produced by a cohort of n sons if all are co-husbands (from Table 1) and if one son is excluded from estate polyandry (from Table 4).

0.4 more offspring on average than it apparently does in order to make inclusion of the h^{th} brother yield an inclusive fitness gain (assuming the junior brother can father 0.54 offspring on his own). Joiners are an estimated 1.6 offspring above the isofitness threshold, while grandparents are about 0.5 offspring above. As for the isofitness value for e —the expected offspring for brothers excluded from estate marriages—this averages slightly below zero for members. That is, given the observed estate family sizes, even if younger brothers excluded from the estate had no chance at all of fathering children, elder brothers would still lose inclusive fitness by including them in the marriage. For joiners and grandparents, the average value of e needed to break even (1.6 and 1.0, respectively) is well above the empirically estimated value of 0.54. Overall, then, the isofitness analysis suggests that there is a comfortable margin around our estimates of p_h and e within which the qualitative results discussed above should continue to hold.

There are of course a number of cautions to keep in mind in interpreting these results. Given the small number of marriages in the sample, it could be that the values used for one or more variables are very poor

Table 5. Isofitness Values for Polyandry and Exclusion (Zangskar)

Number of co-husbands (h)	Observed offspring	Polyandrous family size (p)			RS of excluded brother (e)		
		Member ^a	Joiner ^b	Grandparent ^c	Member ^d	Joiner ^e	Grandparent ^f
Monogamy (1)	3.75						
Diandry (2)	4.8	5.46	3.11	4.29	-0.5	1.78	1.05
Additional (3-4) ^g	5.78	5.76	4.36	5.31	0.47	1.39	1.00
Polyandry (2-4) ^h	5.19	5.58	3.61	4.70	-0.11	1.63	1.03

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^aOffspring from polyandrous union of h co-husbands needed to equal inclusive fitness of union with $h - 1$ co-husbands plus 1 excluded brother. (Solve for p , using equation 5.)

^bOffspring from polyandrous union with h co-husbands needed to equal inclusive fitness obtained if excluded from this union by $h - 1$ brothers. (Solve for p , using equation 6.)

^cOffspring from polyandrous union of h sons serving as co-husbands needed to equal number of grandchildren obtained if one brother is excluded from this union (see Figure 1).

^dOffspring of excluded brother needed to equal inclusive fitness of including him in polyandrous estate union. (Solve for e , using equation 5.)

^eOffspring of excluded brother needed to equal inclusive fitness of being included as i^{th} brother in polyandrous estate union. (Solve for e , using for e , using equation 6.)

^fOffspring of excluded son (e) needed to equal number of grandchildren obtained if this son is included as i^{th} co-husband in polyandrous estate union. (Solve for e , using equation 5.)

^gWeighted average for families indicated.

estimates of the actual universe of values experienced by Zangskar families.¹¹ Clearly, we will need more robust samples, preferably with data on individual family histories, in order to assess the inclusive fitness consequences of Tibetan polyandry. Even so, the framework presented in this paper should be useful in analyzing any richer corpus of data.

Another issue is the assumption that co-husbands have equal probability of fathering the offspring of a polyandrous marriage. Indeed, it seems likely that elder brothers father a disproportionate share, both because of earlier reproductive maturity of the elder brother (Crook and Crook 1988:110, 1994:774ff.; Levine and Silk 1997:383) and because labor schedules may be arranged by seniority so that younger brothers are absent for trading or herding more often. Since Crook and Crook (1988) do not provide any estimates of Zangskar paternity skew, we cannot examine this question directly. However, it is instructive to consider the results supposing the paternity skew documented for Nyinba (Levine and Silk 1997) also holds for Zangskar.¹² Applying this estimate to the data on Zangskar diandry, we find that the isofitness value for senior brothers drops from 5.46 to 5.27, while for junior brothers it rises from 3.11 to 3.23. The first figure is still above the observed diandrous family size average of 4.8; the second is still well below it. Looked at another way, we can say that for the Zangskar data set, a paternity skew of 69% would be sufficient to make diandry pay for senior brothers, while the skew could be increased to 98% without making self-exclusion adaptive for junior brothers. In sum, in Zangskar the skewing of paternity toward elder brothers is likely to provide a net gain in their inclusive fitness without reducing the inclusive fitness of junior co-husbands below the joiner isofitness threshold.

Before turning to broader issues, it is useful to examine the only other direct test of the inclusive-fitness hypothesis for Tibetan polyandry published to date. This test, by Beall and Goldstein (1981; Goldstein and Beall 1982), utilizes data Goldstein collected in Tsang village, Limi Valley, Nepal. Beall and Goldstein (1981) claim that the Tsang data falsify the hypothesis that polyandry (at least in this case) serves to increase the inclusive fitness of its practitioners, instead revealing that polyandry "in fact seems to entail substantial reproductive sacrifice" (1981:11). Specifically, they argue that brothers who marry polyandrously raise fewer children *jointly* that they could *each* raise singly, a finding that if correct obviously does not need further analysis to falsify the inclusive-fitness-enhancement hypothesis. However, there are some problematic features of the Beall and Goldstein analysis that require examination.

First, the figures Beall and Goldstein present on Tsang female fertility categorized by age class and marital status do not correspond to those that Goldstein (1976, 1977) has previously published (Table 6). In particu-

Table 6. Surviving Offspring among Women Aged 45+, Tsang Village, Limi Valley, Nepal^a

Marital status	Number of women	Number of offspring	Mean number of offspring
Monogamous	8 (13) ^b	33	4.1 (4.3) ^b
Polyandrous	4	22	5.5 (4.0)
Unmarried	3 (4)	4	1.3 (1.0)

^aRaw data from Goldstein (1976:Tables II and III); means calculated directly.

^bFigures in parentheses from Beall and Goldstein (1981:Table II); see text, note 12.

lar, the fertility of polyandrously married women aged 40–44 and those aged 45+ is substantially higher in the earlier publications than in Beall and Goldstein 1981.¹³

Second, in comparing the fitness of polyandrous versus monogamous males, Beall and Goldstein assume that *each* male in a cohort of brothers would attain the RS of a sole heir to an estate (what I have defined above as parameter *m*) were he to forgo polyandry. This is a highly questionable assumption. They defend it by noting three facts: (1) there is a pool of unmarried women in the Limi population; (2) polyandry is characteristic of the wealthier peasantry, not the poorest stratum; and (3) all brothers who fissioned from the estate household were able to marry and raise families. Of these facts, only the third is of much relevance, and it is partially contradicted by their own statement (1981:10) that one of the two unmarried adult males in Tsang is “a middle-aged man who recently split off from his brother.” Since neither that paper nor others by Goldstein present detailed data on the frequency of partitioning, monastic celibacy, or outmigration by Tsang males, it is difficult to evaluate this claim in any precise manner. In any case, the proper measure needed to evaluate the tradeoffs involved in polyandry is the RS of brothers who are not included in (polyandrous) estate marriages (the parameter *e* discussed above), which cannot be found in any of Goldstein’s publications. Beall and Goldstein have assumed that $e = m = 4.3$, whereas Crook’s data from Zangskar suggest that $e = 0.15m$, or an estimated value for Tsang of ≈ 0.6 .¹⁴

Third, Goldstein’s own arguments in other publications give a very different picture of the ecological and reproductive constraints involved in Tibetan polyandry. Specifically, Goldstein (1978:329) argues that under the circumstances traditionally experienced in Limi Valley, upon partitioning “the inheritance a younger brother receives is not likely to generate a resource base adequate for economic independence,” owing primarily to scarcity of arable land and the vagaries of animal herding. Thus, in the past, younger brothers adhered to polyandrous marriage

because they saw the partitioning option as too economically costly: “Under what circumstances, then, might younger males perceive the opportunity costs of fission as not prohibitive? Traditionally, there are very few indeed” (Goldstein 1978:330). Goldstein goes on to note that recent changes in Limi’s political-economic context have created expanded non-agricultural opportunities for livelihood. “Given such new opportunities, it is not surprising to find that roughly 25 per cent of the younger brothers [in Limi estate households] actually left their natal family corporations and established neolocal independent family units during the period from 1960–1970” (Goldstein 1978:332). He thus indicates that land is a significant, though not the sole, constraint on reproduction, as evinced by above quotations as well as his remark that “unmarried females do not have enough land even to support themselves, let alone their children” (Goldstein 1977:51). Unmarried Limi women support themselves and their offspring via their own labor (e.g., in weaving) as well as with small stipends from the fathers of their children, but according to Goldstein these sources are only sufficient to support one or two offspring. (The mean number of surviving offspring for three post-menopausal unmarried Tsang women is in fact 1.3, the maximum being 2.)

In sum, the high RS of monogamous estate marriages in Limi is by no means sufficient to disprove the adaptive value of polyandry, and in fact it indicates just the opposite—that estate resources had very positive reproductive consequences. Under the traditional economic system in which polyandry is preferred, the options for reproducing outside of estate marriages appear to be decidedly inferior. While in some instances households formed by partitioning an estate may be viable (Levine and Silk 1997), if arable land is scarce the limit of viability would surely be breached after a few generations of such partitioning (as simulated by Durham 1991:82ff.; see also Crook and Crook 1988:102ff.; Goldstein 1978:330).

METATHEORETICAL ISSUES: MECHANISMS VS. ADAPTIVENESS

Thus far we have been concerned with the adaptiveness of Tibetan polyandry on the assumption that the question is a sensible one. But certain critics, while not rejecting Darwinian analyses of human behavior in general, suggest that phenomena like Tibetan polyandry are not reasonably viewed as adaptations, regardless of what the data on inclusive fitness might reveal. Indeed, one of these critics, Donald Symons (1989, 1992), has singled out the Crook and Crook study as exemplifying what is wrong with what he terms “Darwinian anthropology” or “Darwinian

social science," in contrast to his preferred approach of "Darwinian psychology" or "evolutionary psychology."

This section, then, aims to examine these larger metatheoretical issues—questions about the proper framework for investigating human behavioral adaptation, and about the meaning of such an enterprise in general. Although there are several prominent commentaries on this issue, given Symons's explicit discussion of the Tibetan polyandry case and the comprehensive nature of his criticisms, I think it sensible to focus on his publications. These writings make four claims with which I am concerned here:

1. Extant adaptive explanations of Tibetan polyandry (e.g., Crook and Crook 1988) refer to selective factors that did not exist in the evolutionary past.
2. The proper objects of Darwinian analysis are specialized psychological mechanisms shaped by natural selection, and no such mechanisms have (or plausibly can be) identified that are specific to polyandry.
3. Evolutionary forces such as kin selection cannot be invoked to explain polyandry unless there is reason to believe that specific genes linked to polyandry have been selected by such a force (and given claims 1 and 2, there is no such reason).
4. Data on reproductive differentials are in general irrelevant to understanding adaptations, and particularly so in the polyandry case.

Clearly, if these claims are correct, then Tibetan polyandry cannot be explained in adaptationist terms. Many seem to have tired of the "Darwinian anthropology versus evolutionary psychology" debate that Symons initiated, and have moved on to more productive and collaborative matters. While I do not wish to perpetuate unnecessary disputes, it also does not seem responsible to ignore Symons's criticisms, particularly since he has deployed them in criticizing adaptationist analysis of Tibetan polyandry, and his views have been quite influential. I will consider each of the four arguments in turn.

Would Polyandry Have Been Favored in the EEA?

A key assumption of Symons's critique is that owing to rapid cultural and ecological change we are (genetically) adapted to an "environment of evolutionary adaptedness" (EEA) that disappeared several thousand years ago. According to Symons (1989:138–139), it follows that

a well-formed description of an adaptation must consist *solely* of words for things, events, relations, and so forth, that existed in the EEA, which, in the case of human beings, means the Pleistocene world of nomadic foragers [emphasis in original].

Since this passage was published, several extended critiques of the EEA in general, and Symons's views in particular, have appeared (Alexander 1990; Foley 1995; Irons 1990, 1998; Turke 1990). They have raised several major objections to Symons's position. Rather than review them comprehensively, I will focus on what is relevant to the question of polyandry's adaptive significance.

First there is the matter of characterizing "the Pleistocene world of nomadic foragers." The Pleistocene lasted nearly two million years, during which time hominids underwent multiple speciation events, and the surviving species colonized the entire planet except for the high arctic and oceanic islands. In the process, our lineage adapted to a tremendous variety of habitats (Gamble 1994; Potts 1996). Judging from extant foragers as well as archaeological evidence, Pleistocene foragers developed a range of social systems, subsistence systems, mating patterns, and so on, not all of them matching the stereotype of nomadic band societies. The idea that before agriculture all humans lived in a single type of society is simply untenable (Kelly 1995). Given these facts, we can expect that selection in the hominid lineage favored cognitive mechanisms for adaptive problem-solving and facultative responses to a large variety of social and ecological situations (e.g., Tooby and DeVore 1987). Indeed, the tremendously successful Pleistocene expansion of *Homo sapiens* into diverse habitats without extensive morphological-physiological diversification strongly suggests that our species had already evolved a suite of cognitive-behavioral capabilities for this sort of phenotypic adaptation.

Second, there is the question of specifying what selective forces might have favored the ability to vary mating systems in an adaptive manner. According to Symons, Tibetan polyandry cannot be understood in adaptive terms since it is a response to a host of things—"agricultural estates, animal husbandry, primogeniture, monasticism, aristocrats, landlords, governments, and taxation"—that simply did not exist "in the human EEA." But phrased in somewhat more abstract terms—e.g., resource scarcity, kin cooperation, parental control of mating choices—the case against viewing Tibetan polyandry as an adaptive response to particular conditions is not so compelling. Is the spinal reflex that makes me jerk my hand away when it brushes against an electric waffle iron not an adaptation because nomadic Pleistocene foragers lacked waffle irons or electricity? Obviously the problem here is that I have phrased the question too specifically; rather than waffle irons and electricity, I should talk about danger-

ous heat sources, etc. But what is obvious in the waffle-iron case might not be so obvious in other cases with more complex causal processes (such as Tibetan polyandry). Put another way, novel environmental features (e.g., waffle irons, agricultural estates) may have fitness *effects* very similar to features found in the EEA (e.g., hot embers, economically defendable resource patches). Furthermore, novel and ancient selective features may affect decisions in similar ways, by acting via a *common pathway* of some sort—cognitive mechanisms that categorize multiple stimuli (e.g., objects that cause intense external pain, diverse opportunities to gain or lose status or mates) according to their fitness-related consequences.

The general argument advanced here is that evaluating whether contemporary phenomena match any found in the EEA requires us to specify the adaptive context quite carefully. What is the suitable level of abstraction for analyzing the adaptive significance of Tibetan polyandry? There is no single answer to such a question inherent in the logic of selectionist explanation. On these grounds alone, Symons's dictum is inherently ambiguous—that is, its application necessitates interpretation and judgment, and ultimately much more empirical knowledge about human psychology and decision-making than we can presently lay claim to.

How Specialized Must Evolved Psychological Mechanisms Be?

According to Symons (1992:147),

polyandry, like all human activities, results from the operation of some array of brain/mind mechanisms; but polyandry is an *adaptation* only if at least one of these mechanisms was designed by selection specifically to produce it. In other words, it is an adaptation only if at least one psychological mechanism owes its form to the greater reproductive success of individuals who married polyandrously, in certain circumstances, in ancestral populations. If no such specialized mechanism exists, polyandry is not an adaptation, even though it may currently be adaptive—i.e., fitness-promoting—in certain modern environments. [emphasis in original]

It is logical and conventional to define an “adaptation” as something specifically designed by natural selection, as Symons does; the further specification that behavioral adaptations must be produced by a specific psychological mechanism that was designed *only* to produce it is a further step that is relatively unique to the program of evolutionary psychology.

Behavioral phenomena are relatively ephemeral aspects of phenotype, whereas underlying cognitive mechanisms are more stable and lie closer (in the causal pathway) to the genes. As Tooby and Cosmides (1990:396–397) put it,

One reason why the avunculate, the English language, cross-cousin marriages, and Tibetan polyandry cannot be adaptations is because they vary from human to human in a way that is not (plausibly) caused by genetic differences between them. These are expressions of adaptations, but not adaptations themselves.

Perhaps what we have here is primarily a semantic problem: do not apply the label “adaptation” to phenotypically variable phenomena (e.g., sun-tanning), only to the underlying mechanisms that produce them (e.g., the physiological basis for being able to tan). Symons et al. are objecting to the polyandry-is-adaptive argument by arguing that polyandry is not an *adaptation* (because it cannot be linked to specific genes and a dedicated polyandry-only cognitive mechanism). Fine, but this begs the question of whether the facultative ability to establish polyandrous marriages is deployed in an adaptive (fitness-enhancing) manner, and in a way that implies adaptive design. More directly, it bears pointing out that the logic of Crook and Crook's analysis (as of mine) is that instances of polyandry in certain particular circumstances are expressions of an adaptive decision rule (to put it in simple and rather metaphorical terms); it is this decision rule rather than polyandry itself which is the hypothesized adaptation. Thus, I find this part of the critique rather misplaced.

But let's return to the issue of whether we need to posit a dedicated (polyandry-specific) cognitive mechanism in order to view polyandry as a product of adaptation. The evolutionary psychology proposal that many adaptive problems are handled by dedicated (domain-specific) psychological mechanisms is a plausible one. But I find it equally plausible that cognitive mechanisms which enhance fitness in a broad range of socio-ecological contexts, with perhaps a broad array of behavioral manifestations, have also evolved. Indeed, I find this view more consistent with the ethnographic evidence than the suggestions that any adaptive variation in human mating systems (or avian ones, for that matter) is based on specialized cognitive mechanisms. Of course, such broadly adaptive mechanisms may not in fact exist: maybe the right gene combinations never arose, maybe such a mechanism is too expensive, maybe it is an impossible design problem, and so on. But the *presumption* that all adaptive mechanisms must be highly domain-specific—the “one domain, one algorithm” assumption implied by Symons and some other evolutionary psychologists—has no clear logical or empirical superiority. Rather, I would say that determining the degree of domain specificity in human psychological mechanisms is basically an empirical issue that must be tackled with a suite of inquiries, ranging from primarily psychological ones to those focused on fitness consequences.

What evolved mechanisms could plausibly underpin facultative deployment of polyandry in an adaptive manner? This is the more specific

issue posed by Symons's critique of Crook and Crook (1988). Ethnographic evidence (reviewed in Levine and Sangree 1980; Cassidy and Lee 1989) indicates that polyandry occurs in a number of widely separated human populations, including some foragers (e.g., Eskimo, Paiute, and Shoshone). The general context is often the same: shortage of long-term mating opportunities for males, as defined by local social and economic constraints on marriage and resource control, coupled with some significant advantage to (generally fraternal) male cooperation.¹⁵ But given the rarity of polyandry, and the rather special circumstances under which it occurs, I share Symons's skepticism that humans possess an evolved cognitive mechanism specific to it.

The far more plausible alternative is that polyandry is an expression of one or more psychological mechanisms that allow humans to track local environmental conditions and vary mating and kin-affiliation strategies according to fitness-correlated payoffs. While the exact nature of such mechanisms is unknown, we need not postulate the all-purpose "inclusive fitness maximizing algorithm" that Symons and others have ridiculed. A promising line of theoretical and empirical work focuses on the fundamental life-history trade-off between wealth/status acquisition and parental investment, proposing that (in contrast to, say, the average primate) human socioecology often favors a trade-off toward reduced reproduction (Borgerhoff Mulder 1998; Kaplan et al. 1995; Rogers 1990). In any case, our current ignorance of psychological mechanisms governing such trade-offs need not prevent us from hypothesizing that they exist and indirectly testing such a hypothesis or postulate by analyzing adaptive variation in reproductive strategies (including polyandry).

While such a research strategy is obviously incomplete, and postpones the investigation of the underlying cognitive mechanisms, this is in principle no different than the near-universal practice among students of human behavioral adaptation (including evolutionary psychologists) of provisionally setting aside investigation of the specific gene complexes and neurophysiological pathways that might underlie proposed adaptive regularities in the human psyche and behavior.¹⁶ Furthermore, this ambiguity concerning specific mechanisms is in fact quite characteristic of many studies in evolutionary psychology. Consider the oft-propounded female preference for marrying men of high status. Since this is observed to occur in a wide variety of cultures (e.g., Buss 1989), one might infer that the mechanisms producing it must be general enough to perceive a wide variety of stimuli (e.g., monetary wealth, fighting prowess, political standing, agricultural land, hunting ability), many of which did not occur in the Pleistocene, as indices of male status. Thus, Symons (1992:143) is willing to postulate a "psychological adaptation that specifies the rule 'prefer signs of high status'" even though "the particular correlates or

indexes [*sic*] of male status do, of course vary." But alternatively one could postulate a psychological adaptation that specifies the rule "Teach your daughters to prefer mates who are locally successful and will maximize their chances to raise a family," or a rule of the form "Prefer long-term mates who give evidence of predilection to high parental investment, and short-term mates who have good resources or high-quality phenotypes." We don't know which of these is more likely to match the underlying cognitive algorithms that account for the cross-cultural observations. In any case, they all are rather more generalized (in terms of stimuli responded to and behavioral outputs used to follow them) than the "specialized polyandry-producing mechanism" Symons wants to see before he'll accept any adaptive explanations for polyandry.

In sum, I confess my ignorance concerning the psychological mechanisms underlying facultative adaptive behavior (e.g., choosing high-status husbands, marrying polyandrously), but suppose that it emerges from a complex, poorly understood process involving (1) genetically evolved learning biases (the domain-specific algorithms of evolutionary psychology); (2) higher-level (relatively domain-general) cognitive processes such as scenario-building and targeted social learning (e.g., imitation of locally successful strategies); and (3) undirected cultural evolution (e.g., natural selection acting on culturally transmitted variants). Whatever the specific mechanisms, it seems a reasonable hypothesis that in special circumstances (as noted above) brothers might come to believe (through observation, instruction, trial and error learning, and/or cultural evolution) that sharing a wife is the most rewarding mating option available.

Does Kin Selection Presume Genetic Specialization?

The inclusive-fitness-maximization hypothesis often proposed to account for polyandry relies on the notion that reproductive sacrifice by Ego which enhances the RS of close kin can be favored by natural selection under the conditions specified by Hamilton's rule (see above). Although there are cultural analogues to inclusive fitness and kin selection (Werren and Pulliam 1981), almost all usages of these concepts assume implicitly or explicitly that the inheritance mechanism involved is genetic. Given this, some have interpreted such explanations as positing "genes for polyandry" or other specific forms of kin altruism. Thus, Symons (1992:150) approvingly cites a passage in Dawkins (1982:27-28) that criticizes an adaptationist analysis of polyandry (most likely Hiatt 1980) for naively refusing to postulate genes for polyandry. Dawkins argues that one "cannot talk about kin selection, or any other form of Darwinian selection,

without dragging genes in, whether you do so explicitly or not," and warns that "formidable difficulties" face any such analysis, since

either [the] polyandrous tribes had to have been living, in partial genetic isolation, under their peculiar conditions for a large number of centuries, or natural selection had to have favoured the universal occurrence of genes programming some complex "conditional strategy" (Dawkins 1982:28).

In a similar vein, Durham (1991:58) has argued that

kin selection is actually a form of genetic selection and can only explain (or "lead one to expect") behavior when behavioral variation is correlated with genetic variation . . . Thus the [kin selection] argument assumes that there are genetic differences between people who marry in the fraternal polyandrous fashion and those who do not.

It is ironic that Durham—an adaptationist but one highly critical of sociobiology (as he defines it)—allies himself with those like Symons who argue that Darwinian analysis of human behavior must identify unique, genetically evolved, cognitive mechanisms that were selected specifically for the fitness effects produced by the behavior of interest.

But in fact most of those who have invoked kin selection as the cover theory for adaptive explanations of human behavior (including polyandry) have no intention of positing specific genetic differences that cause the behavior of interest to be expressed in one population and not another. As Irons (1979:5) eloquently stated a number of years ago,

The hypothesis that human behavioral propensities are adaptations shaped by natural selection does not imply that human behavior is not plastic or that differences in behavior among human populations are the result of genetic differences. The most reasonable hypothesis is that the behavioral differences exhibited by different populations are environmentally induced variations in the expression of basically similar genotypes (cf. Haldane 1956), and that the ability and propensity to vary behavior in response to environmental differences is itself an adaptation.

Again, the issue here hinges on the *specificity* of the psychological mechanisms (and underlying genetic variation) required or assumed. Put simply, most researchers invoking kin selection to explain a facultative behavior like polyandry are rather agnostic about the specific mechanisms that might be involved, but certainly see no need to assume that the mechanism(s) must be linked to genes that were selected exclusively in order to produce polyandry.

Durham's statement raises a further criticism by stating that kin-selection explanations of polyandry necessarily posit genetic differences between polyandrous and non-polyandrous people. Durham is of course correct that kin selection is "a form of genetic selection" and thus requires

(genetically) heritable differences between those who behave in manner X and those who don't in order for selection to favor the spread of the genes and the linked phenotypes. But these genes need not code for something as specific as polyandry, and even if they did, the adaptively designed phenotype could involve *facultative* polyandry in response to local conditions (the "complex conditional strategy" alluded to by Dawkins). In either case we would neither expect nor require there to be "genetic differences between people who marry in the fraternal polyandrous fashion and those who do not."

In my estimation, Durham's insistence that kin selection requires that *current* genetic variation determine the presence or absence of polyandry has more to do with the politicized debate over sociobiology in the late 1970s than with contemporary practice in evolutionary behavioral ecology, human or otherwise. For example, a fair number of bird species exhibit facultative polyandry (e.g., Chao 1997; Davies and Hartley 1996; Whittingham et al. 1997); to my knowledge, few if any students of avian polyandry assume that current genetic differences between individuals or populations of the same species must account for this phenotypic variation. In truth, we know very little about the ontogeny and behavioral genetics of complex and adaptively significant social behavior in vertebrates, including humans. That is a sign of our ignorance, but it is not good grounds for ruling tests of adaptationist hypotheses out of court until such ontogenetic information is securely established.

I would further argue that an insistence that any adaptive analysis of polyandry implies "genes for polyandry" would seem to return us to a narrow and outmoded conception of behavioral ontogeny and evolutionary explanation, circa 1950 and the heyday of classical ethology with its "fixed action patterns" and "innate releasing mechanisms." Certainly such tightly controlled ontogenies and highly specific stimulus-mechanism-behavior linkages do exist, including in humans (e.g., aversive conditioning to novel foods following nausea), but I doubt they will explain more than a minor fraction of human social behavior. Increasingly, evolutionary psychology is moving towards more complex and contextual models of cognitive mechanisms, and I suspect this part of Symons's critique has few current adherents.

What Is the Significance of Reproductive Differentials?

Since we lack time machines or detailed knowledge of the evolutionary past, we are forced to make inferences about whether a given aspect of phenotype exists because it enhanced the fitness of past bearers. One way to make such inferences is to measure the *current* fitness consequences of

the trait under investigation, in order to see whether it does indeed do better than the alternatives. But critics like Symons (e.g., Kitcher 1985; Tooby and Cosmides 1990) rule this improper. According to Symons (1989:139),

measuring reproductive differentials among individuals who do and do not marry polyandrously is irrelevant. Reproductive differentials would be significant only if they constituted evidence for the existence of, or nature of, a specialized polyandry-producing mechanism in the human psyche.

He further states that

there is no reason to suppose that Crook and Crook's reproductive data will—or should—prompt other students of polyandry to question or modify previously held assumptions about human psychology. Indeed, there is no particular reason to suppose that Crook and Crook's reproductive data have any bearing on the anthropology of polyandry; they simply argued that polyandrous marriages are fitness-promoting in certain highly unusual circumstances (Symons 1992:147).

At least three distinct issues are raised here: (i) Do data on differential reproductive success (RS) provide evidence of "a specialized polyandry-producing mechanism in the human psyche"? (ii) Do these data imply a view of human nature different than the received anthropological wisdom? (iii) Do they provide a valid means to test hypotheses about adaptation?

To the extent that my arguments above concerning the specificity of mechanisms underlying polyandry are valid, I believe I have blunted the first question. Both the first and second question illustrate Symons's view (held by many other evolutionary psychologists) that study of psychological mechanisms is *the* subject in evolutionary analyses of human behavior; though I find that highly debatable, I will pass it over and turn to the more specific question of what an analysis like Crook and Crook's (or mine) implies about human psychology in general. I believe such analyses are predicated on the notion that humans are equipped with a set of psychological mechanisms that allow them to arrive at patterns of behavior that track environmental variation in fitness-enhancing ways. Put another way, the implicit assumption is that the human psyche is designed to process inputs developmentally and cognitively in ways that produce locally adapted behavior. This view, common to behavioral ecology (Grafen 1984) as well as "Darwinian anthropology," is admittedly "mechanism-agnostic" (Symons 1992:155). Whereas Symons thinks this is a bad thing, at least when the mechanisms are psychological, I do not (Smith 1987:227ff.; see also note 16, *supra*).

Be that as it may, the "view of human psychology" assumed by human behavioral ecologists is significantly divergent from the "standard social

science model" (Tooby and Cosmides 1992). The latter holds that people learn, adopt, choose, or invent that which is conventional to their socio-cultural milieu or that which perpetuates certain social, cultural, or symbolic entities, while the phenotypic adaptation approach of behavioral ecology and allied views postulates that people learn, adopt, choose, or invent options that will enhance their probability of surviving and reproducing in local socioecological contexts. The behavioral ecology view of human nature thus predicts a very close and detailed positive correlation between local behavioral variation and fitness payoffs (though it does not expect that people consciously or unconsciously seek fitness payoffs themselves, only their proximate correlates). Although the various theoretical schools in sociocultural anthropology and other social sciences differ amongst themselves in what patterns they expect to find in human behavioral variation, none of them besides the one Symons is attacking expect it to correlate with fitness consequences. Indeed, the anthropological debate over Tibetan polyandry (reviewed above, and more fully in Durham 1991) clearly indicates that Crook et al.'s adaptationist stance conflicts with the expectations generated by conventional social science. Hence, I believe Symons to be quite mistaken regarding question (ii); he has conflated agnosticism about specific psychological mechanisms with agnosticism about human motivation or learning in general.

Finally, does "counting babies" (as some disparagingly phrase it) offer a valid means of testing hypotheses about adaptive phenotypic variation? Symons (1990, 1992:148f.) offers seven reasons why he believes "correlating individual variation in the expression of a trait with reproductive success is normally an ineffective or ambiguous way to study adaptation." This issue has been widely debated in recent years, and most participants in the debate are rather sick of it and have gone on to other concerns, so I will be brief (see reviews by Blurton Jones 1990; Borgerhoff Mulder 1991; Borgerhoff Mulder et al. 1997; Clutton-Brock 1988; and Sherman and Reeve 1996).

There is no question that correlations between RS and the expression of phenotypic traits can be misleading about the adaptive significance of these traits owing to such problems as phenotypic correlation (see above), adaptive lag (changes from the EEA), measurement or sampling error, and so on. But most evolutionists—including Symons (1992:148)—realize that such correlations can also be revealing. In behavioral ecology, the usual practice is to use proximate currencies (e.g., mating frequency, energy capture rate) in hypothesis testing because of difficulties in measuring lifetime RS and concerns such as those listed above, plus the realization that organisms are after all using such cues rather than RS or fitness per se in evaluating or responding to alternatives. In some cases, however, it is difficult to identify plausible proximate currencies, and RS is the most

reasonable measure of adaptive outcome. I believe this is the case with regard to assessing the adaptive significance of Tibetan polyandry, but I would welcome alternative tests that use other appropriate currencies.

Would Cultural Evolution Produce Adaptive Polyandry?

Darwinian psychology as conceptualized by Symons presumes that adaptive behavior must arise from genetically evolved, highly domain-specific mechanisms. This may be the most direct way to apply Darwinism to human behavior, but it's not necessarily the only fruitful way. If certain beliefs and preferences affecting the likelihood of polyandry are culturally heritable (and as with genetic inheritance, heritability need not be 100%, nor need it exclude either human agency or genetically evolved learning biases), then it is possible that polyandry could evolve through natural selection and other evolutionary forces (Boyd and Richerson 1985) acting on cultural variation.

Indeed, the most frequently proposed adaptive explanation for Tibetan polyandry is that a "monogamous principle" (Goldstein 1971) is followed in order to prevent division at inheritance from depleting an estate's land base below the viable size, and brothers are encouraged to marry polyandrously in order to reap the advantages of cooperative division of labor (Alexander 1974; Durham 1991). This explanation is similar to the hypothesis I have formalized and tested above. At least some versions of the estate-preservation explanation differ from it in subtle but important ways, however. In particular, explanations that focus on the *long-term* adaptiveness of polyandry are hard to anchor in the nepotistic and selfish decisions of individual actors, for these explanations accept that in the short run (i.e., within a lifetime) a participant's inclusive fitness would be enhanced if he avoided polyandry. What has been selected for, it is thus argued, is the long-term preservation of lineages and their agricultural estates (Durham 1991). Such an explanation requires an explicit *inheritance mechanism* through which selection acts over multiple generations. If (for reasons discussed above) a specifically genetic mechanism is implausible, what about cultural inheritance?

In this case, I expect that estate persistence, rather than inclusive fitness *per se*, would be the variable maximized. The scenario for the cultural evolution of a monogamous principle is speculative, involving a process whereby those estate-owning families who developed a monogamous principle would leave more estate-owning descendants than those who had not yet developed or adopted such a rule (Crook and Crook 1994; Durham 1991). These descendants would in turn transmit this meme-complex (presumably a conditional rule valuing adherence to polyandry

whenever it leads to economic and perhaps reproductive rewards) to their estate heirs. After a number of generations, those adhering to the monogamous principle would monopolize the estate-owning niche while the (possibly more numerous) descendants of those who had never adopted this principle would disperse into the landless segments of the regional population.

Thus, in the cultural evolutionary dynamic just sketched, the monogamous principle (and associated high frequency of polyandrous marriage) might be evolutionarily stable given the particular selection regime and transmission structure encountered in the high-altitude low-productivity agropastoral niche of Tibetans. This could be true even if the average inclusive fitness of those adhering to the monogamous principle was lower than before the spread of the monogamous principle. Whether one wants to call this an "adaptive explanation" or not is a semantic matter; I certainly think it is a selectionist one in any case.

The psychological mechanisms that presumably underlie such an evolutionary scenario are those that make family living, paternal investment, resource control, and cultural learning prominent features of many human societies. It is these mechanisms, coupled with the capacity for cultural transmission of phenotype-shaping information (Boyd and Richerson 1985), and interacting with relatively rare social and ecological settings, that I hypothesize would drive the cultural evolution of Tibetan polyandry. While speculative, this argument seems worthy of more rigorous formulation and empirical test, as has been initiated by Durham (1991) and Crook (1995). What remains elusive is an adequate account of why so few populations with the characteristics outlined above have widespread polyandry. Why in Tibet but not in the Andean altiplano or the agropastoral zones of northern Europe? Rather similar constraints concerning land inheritance and partibility have been met by monogamous rules that specify unigeniture rather than polyandry (Boone 1986; Goody 1976). Perhaps historical and cultural constraints unique to Tibet account for this pattern, but they have yet to be fully explicated.

CONCLUSION

In an attempt to evaluate various arguments over the adaptive significance of Tibetan polyandry, this paper has ranged over diverse methodological, analytical, and metatheoretical terrain. I have argued that previous analyses of the inclusive-fitness consequences of fraternal polyandry are weakened by a number of methodological problems. In particular, these problems involve failure to take into account the lowered

coefficient of relatedness of fraternal co-husbands produced over previous generations of polyandry, to specify realistic outcomes for non-polyandrous options (particularly exclusion from estate marriage), and to distinguish the different reproductive interests and opportunity costs faced by senior vs. junior brothers.

With respect to the metatheoretical issue, I have made the following arguments: (1) The specificity of evolved psychological mechanisms is primarily an empirical matter, contrary to the views of some evolutionary psychologists that these mechanisms must all be highly specialized. (2) The notion of the "environment of evolutionary adaptedness," although useful in principle, has severe ambiguities in practice. (3) Mechanisms that would produce adaptive variation in mating systems within stratified agricultural societies could plausibly have evolved in pre-agricultural socioecological conditions. (4) Hence, critiques by Darwinian psychologists of Darwinian anthropology in general, and of adaptationist analyses of Tibetan polyandry in particular, are not well founded. (5) However, precise adjustment of the incidence and intensiveness of polyandry so as to maximize inclusive fitness effects might require more specific decision-making mechanisms than are likely to have evolved either genetically or culturally; this too is a primarily empirical question.

Despite this last caveat, the analyses reported here confirm and extend the tentative conclusion reached by Crook and Crook (1988) that "men who marry polyandrously may not necessarily lower their individual fitness greatly." Their data from Zangskar, Ladakh, when reanalyzed using the methods presented herein, indicate that while senior brothers ("members") may suffer small declines in inclusive fitness by sharing wives and estates with junior brothers ("joiners"), junior brothers as well as parents of a set of fraternal co-husbands experience inclusive fitness gains from the practice (under traditional economic conditions). Comparative data from other ethnically Tibetan populations (Nyinba, Limi) are insufficient to test the member-joiner model, but the fact that the relevant parameters which can be calculated from published data closely match the Zangskar case suggests these other cases may also conform to Hamilton's rule. Based on the evidence at hand, Tibetan polyandry seems to be just what Alexander (1974), Crook and Crook (1988), Durham (1991), and Goldstein (1976) have claimed it is: a rare but adaptive system for preserving family estates, and hence reliably supporting lineal descendants, across the generations.

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NOTES

1. For additional information on the sample and discussion of its implications, see Crook and Crook (1994), Crook and Shakyia (1994), and Crook (1995). Note that the figure of 3.63 given in Crook and Crook (1994:770) as the mean completed family size for monogamous *khang.chen* families is in error; it should be 3.75, as listed in Crook and Crook (1988).

2. This is 0.2 more offspring than Crook and Crook (1988:109) report; although their equation is correct, their computation contains a minor error in arithmetic.

3. In a later publication, Crook and Crook (1994:773f.) independently note this problem, and its effect in lowering r between co-husbands to an equilibrium value near that of half-sibs (i.e., 0.375). They also note that this will raise the polyandrous family size needed to achieve isofitness.

4. In evaluating Table 3, several points should be kept in mind. Goldstein's (1971) demographic reconstruction of Chimbrow villagers from Tibet, conducted in a refugee community in India, sampled 62 estate marriages, of which 29 were monogamous (5 of these uxori-local), 24 diandrous, 7 triandrous, and 1 tetrandrous, with a final (uxori-local) marriage consisting of sororal polygyny; this yields a total of 103 co-husbands and one co-wife in 62 marriages, from which the figures in Table 3 could be calculated. Goldstein (1976) subsequently conducted a study of ethnic Tibetans in Limi Valley, northwestern Nepal, but these data do not provide frequencies of each type of polyandrous marriage, so equilibrium values of h and r could not be estimated. Nancy Levine's data on the ethnically Tibetan and polyandrous Nyinba of Humla district in northwestern Nepal also yield an arithmetic mean of 1.68 co-husbands, for censuses conducted in 1974 (224 husbands/133 wives) and in 1983 (280/167) (Levine 1988:145); these samples include 5 and 9 cases, respectively, of polygyny as well as some instances of polygynandry. The data on the 1983 census given in Levine's Tables 7.1 and 7.3 were used to calculate the values of h and r listed in my Table 3. Using a slightly revised version of the 1983 tabulation, Levine and Silk (1997) calculate the mean number of co-husbands to be 3.5, but this is for (ever-)polyandrous marriages only, leaving out the monogamous cases, which totaled 45% of all marriages in the 1983 census (Levine 1988:144). Using a different method than was adopted here, Levine and Silk estimate r in this population to be 0.357, but this value excludes monogamous

estate marriages. For reasons given in the appendix to this paper, I feel it is imperative to include monogamous cases in calculating the expected or equilibrium value of r for co-husbands in any population with recurrent polyandry.

5. The reduction is calculated from the difference between the r of Ego to his full sib's offspring (0.25), and that to the offspring of a part-sib, which will be half the r between Ego and the part sib. In the present case this is equal to $1 - (0.233/0.25) = 0.07$. Since inclusive fitness realized through effects on non-descendant relatives is always a product including r as one of the terms, the 7% reduction holds regardless of the other variables in the fitness calculations.

6. This was calculated as follows: (a) from Crook and Crook (1988:Table 5.3), we see that there are 37 men married monogamously or polyandrously in *khang.chen* (patrilocal estate) unions, while another 7 are in minor (*khang.chun*) marriages, for a total of 44 married men; (b) according to Crook and Crook (1988:104), "in Zangskar we do in fact find 30% of brothers are monks"; (c) if we assume these figures include all members of this hypothetical cohort, then it would consist of 63 brothers, 19 of them monks; (d) the 7 men who engaged in non-estate marriages averaged 2.0 children (Crook and Crook 1988: Table 5.3), while I assume the monks, being celibate, leave no offspring; (e) thus, the RS of brothers who do not participate in a major marriage is expected to average $2(7/26) + 0(19/26) = 0.53846$. Crook and Crook (1994) provide more detailed data on a sample of 80 men in sTongde village, Zangskar; of these, 44 (55%) are in *khang.chen* marriages, 6 in *khang.chun* marriages, 2 in *mag.pa* (uxorilocal estate) marriages, and another 28 (35%) are monks. If we assume that *mag.pa* get same RS as monogamous *khang.chen* (i.e., 3.75), and that other categories experience the same average RS as in Leh, then $e = 3.75(2/36) + 2(6/36) + 0(28/36) = 0.54167$. Thus, these two estimates converge closely on an estimated value of 0.54 for e (the expected RS of brothers excluded from estate marriages).

7. Crook and Crook (1988) discuss this multiplicity of interests but do not provide an analysis of them.

8. Crook and Crook (1988) show that women who marry polyandrously obtain higher reproductive success (RS) than those in monogamous unions, suggesting that it is advantageous to be a wife in a polyandrous marriage. On the other hand, a larger number of women than men must necessarily remain unmarried in a marriage market dominated by polyandry. Hence the reproductive interests of women in this system are not simple or easily summarized. Further discussion of married and unmarried women in Tibetan social systems can be found in Goldstein (1976), Levine (1988), and Schuler (1987).

9. Since the third term on each side of equation 6 is identical, the inequality can be simplified by simply deleting them. I left the terms in, however, to clarify the derivation and to highlight the parallel with inequality 5.

10. Indeed, Crook and Crook (1988:110) suggest that "most of the early children in the marriage are sired by the eldest father rather than his teenage brothers" and that second sons are disproportionately likely to become monks, thus increasing the reproductive priority of the eldest-born co-husband. Levine and Silk (1997:383) show that among Nyinba, where paternity ascription is quite detailed (but monastic opportunities scarce), older co-husbands father more children in total as well as per year of marriage, and both differences are statistically significant.

11. The variation in the completed family size data for the 29 Zangskari men in Crook and Crook's study is high (1988: Table 5.3), specifically:

Family Type	Cases	Mean	s.d.	Range
<i>Khang.chun</i>	7	2.0	1.51	0-4
<i>Khang.chen</i>				
Monogamous	12	3.8	2.45	0-8
Diandry	6	4.8	1.95	2-7
Triandry	3	4.7	1.25	3-6
Tetrandry	1	9	—	—
(Polyandry)	10	5.2	2.09	2-9

12. In the Nyinba case, polyandrously married eldest brothers fathered 46% of surviving children, second-borns fathered 38%, and more junior co-husbands fathered the remaining 16% (Levine and Silk 1997: Table 4). Since eldest sons constitute 29% (1/3.5) of polyandrously married co-husbands, the reproductive skew in their favor is considerable, amounting to nearly 60% greater RS than expected if there were no skew.

13. Goldstein (1976:226, 1977:49) lists the four polyandrous women aged 45+ as having 22 living offspring, for a mean of 5.5, while Beall and Goldstein (1981:8) list four women in this category as having a "mean number of surviving offspring" of 4.0, a reduction of nearly 30%. The difference for polyandrous women aged 40-44 is even greater (1976/1977 = 6.0, 1981 = 3.5, though the sample is apparently different: $n = 1$ in 1976/1977, $n = 2$ in 1981). Comparison of the two data sets is complicated by the fact that Beall and Goldstein (1981), unlike Goldstein (1976, 1977), do not include numerical data on age-specific (and marital type) fertility and child mortality, but only averages. While some of the differences between the two data sets are apparently due to recategorization of women by age class (Goldstein 1981:725) and to increases in sample size, some may also be due to computational or typographical errors in Beall and Goldstein (1981), since one error has already been acknowledged (Goldstein and Beall 1982:901) and I have found others. Of particular relevance is that Beall and Goldstein (1981:8) list the "mean number of children ever born" for polyandrous women aged 45+ as 6.3 and the "mean percent offspring mortality" as 69, which would yield a computed mean of 1.953 surviving offspring (vs. the published figure of 4.0); a similar discrepancy arises for the figures given for monogamous women of the same age class (7.8 mean offspring born \times 59% mortality = 4.6 dead and 3.2 surviving, vs. the 4.3 surviving listed by Beall and Goldstein). In sum, since Beall and Goldstein 1981 does not provide raw data, and the figures it does provide contain internal contradictions as well as discrepancies with Goldstein's previously published data, I rely here exclusively on the 1976/1977 figures.

14. In Zangskar, m (the average RS for monogamous estate marriages) is 3.75, while e (the estimated RS for brothers not in the estate marriage) is 0.54, as detailed earlier; thus, since $0.54/3.75 = 0.144$, $e \approx 0.15m$. In the Tsang case, the number of surviving offspring for monogamously married women aged 45+ averages 4.1 ($n = 8$, Goldstein 1976:226; given as 4.3, $n = 12$ in Beall and Goldstein 1981:8). Although it is not clear that all of these offspring are from estate marriages (and a few may be uxorilocal *magpa* marriages), that inference seems approximately correct and hence provides our estimate of p . Thus, lacking any data our best estimate of e is 0.59 (0.144×4.1) or 0.62 (0.144×4.3). Interestingly, the ratio of average RS for estate monogamy to average RS for estate polyandry is $4.1/5.5 = 0.75$ for the Tsang data, very close to the Zangskar figure of $3.75/5.19 = 0.72$.

15. In contrast to cases involving fraternal polyandry such as those discussed

here, systems of non-fraternal polyandry such as are found in certain peoples in West Africa, the Marquesas, and among the Nayar seem to have very different causes, contexts, and consequences (Levine and Sangree 1980; Thomas 1989).

16. Symons (1989:142) argues that "hypotheses about human psychological adaptations can be formulated and tested without speculating about, or knowing anything about, specific neurophysiological processes (see Cosmides and Tooby 1987)." Similarly, some evolutionary psychologists argue that their investigations of adaptive design of the human psyche (and manifest behavior) can proceed without attention to the genetic underpinnings necessarily assumed in their research program. I agree with these views as statements of research strategy in evolutionary analyses of human behavior; but I also would argue that the same exemptions apply to investigations of the adaptive design of behavior that do not specify or investigate presumed underlying psychological mechanisms (see also Alexander 1990; Turke 1990). Put another way, I find the view that adaptationist analysis of the psyche can proceed without knowledge of the genetic or neurophysiological mechanisms that produce it, but behavioral analysis must be tied to specific cognitive mechanisms, inconsistent if not hypocritical.

APPENDIX

Deriving Equations for Relatedness

Alan R. Rogers

In a population practicing fraternal polyandry, two genes drawn from random siblings in generation $t + 1$ will be identical by descent with probability

$$f(t + 1) = \frac{1}{8} + \frac{1}{4}[(1/h)(\frac{1}{2}) + (1 - 1/h)f(t)] \quad (\text{A.1})$$

where h is the number of co-husbands and $f(t)$ is the probability that two random siblings are identical by descent in generation t . This can be justified as follows:

1. The first term accounts for the possibility that both genes came from the mother. For the two genes to be identical this way, the following must be true: (i) gene A came from the mother, (ii) gene B came from the mother, and (iii) A and B were both copies of the same maternal gene. These three events are independent and each have a probability of $\frac{1}{2}$, so the joint probability is $(\frac{1}{2})(\frac{1}{2})(\frac{1}{2}) = \frac{1}{8}$.

2. The second term accounts for the possibility that the two genes both came from males. This happens with probability $\frac{1}{4}$, which accounts for the " $\frac{1}{4}$ " at the beginning. Inside the square brackets, $1/h$ is the probability that the two genes came from the same male and $\frac{1}{2}$ the probability that they are copies of the same gene within this male. Then $(1 - 1/h)$ is the probability that the two genes came from different males and $f(t)$ is the probability that two such genes are identical by descent.

At equilibrium, $f(t + 1)$ must equal $f(t)$. Using the symbol f to represent this common value, we can rearrange equation A.1 as

$$f = \frac{1 + 1/h}{6 + 2/h} \quad (\text{A.2})$$

Thus, polyandry with an infinite number of husbands yields a probability of sharing genes identical by descent that is 25% higher ($f = \frac{1}{6}$) than with the standard half-sib case ($f = \frac{1}{8}$), but 25% lower than for outbred full sibs ($f = \frac{1}{4}$).

If mating is at random, then the coefficient of relationship r between siblings is twice f :

$$f = \frac{2 + 2/h}{6 + 2/h} \quad (\text{A.3})$$

for a line of descent with exactly h fraternal co-husbands in each generation. This simplifies to

$$r = (h+1)/(3h+1) \quad (\text{A.4})$$

which is given as equation 1 in the text.

Since h will in fact vary among families, equation A.1 should be interpreted as an expression involving mean values and will therefore depend on the mean of $1/h$. This is equal to $1/H$, where H is the harmonic mean of h (Crow and Kimura 1970:480). Thus, when h varies, formulas A.1–A.4 are still correct, provided that h is interpreted as the harmonic mean of co-husbands per family.

REFERENCES

- Alexander, Richard D.
1974 The Evolution of Social Behavior. *Annual Review of Ecology and Systematics* 5:325–383.
- 1990 Epigenetic Rules and Darwinian Algorithms: The Adaptive Study of Learning and Development. *Ethology and Sociobiology* 11:241–303.
- Beall, Cynthia M., and Melvyn C. Goldstein
1981 Tibetan Fraternal Polyandry: A Test of Sociobiological Theory. *American Anthropologist* 83:5–12.
- Blurton Jones, Nicholas G.
1990 Three Sensible Paradigms for Research on Evolution and Human Behavior? *Ethology and Sociobiology* 11:353–359.
- Boone, James L.
1986 Parental Investment and Elite Family Structure: A Case Study of Late Medieval-Early Modern Genealogies. *American Anthropologist* 88:859–878.

- Borgerhoff Mulder, Monique
 1991 Human Behavioural Ecology. In *Behavioural Ecology: An Evolutionary Approach*, third edition, J. R. Krebs and N. B. Davies, eds. Pp. 69–98. Oxford: Blackwell.
- 1998 Demographic Transition: Are We Coming Any Closer to an Evolutionary Explanation? *Trends in Ecology and Evolution* 13(7), in press.
- Borgerhoff Mulder, Monique, Peter J. Richerson, Nancy W. Thornhill, and Eckart Voland
 1997 The Place of Behavioural Ecological Anthropology in the Evolutionary Social Sciences. In *Human by Nature: Between Biology and the Social Sciences*, P. Weingart, S. D. Mitchell, P. J. Richerson, and S. Maassen, eds. Pp. 253–282. Hillsdale, New Jersey: Erlbaum.
- Boyd, Robert, and Peter J. Richerson
 1985 *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.
- Buss, David M.
 1989 Sex Differences in Human Mate Preferences: Evolutionary Hypotheses Tested in 37 Cultures. *Behavioral and Brain Sciences* 12:1–49.
- Cassidy, Margaret L., and Gary R. Lee
 1989 The Study of Polyandry: A Critique and Synthesis. *Journal of Comparative Family Studies* 20:1–11.
- Chao, L.
 1997 Evolution of Polyandry in a Communal Breeding System. *Behavioral Ecology* 8:668–674.
- Clutton-Brock, T. H., ed.
 1988 *Reproductive Success: Studies in Individual Variation in Contrasting Breeding Systems*. Chicago: University of Chicago Press.
- Cosmides, Leda, and John Tooby
 1987 From Evolution to Behavior: Evolutionary Psychology as the Missing Link. In *The Latest on the Best: Essays on Evolution and Optimality*, John Dupre, ed. Pp. 277–306. Cambridge: MIT Press.
- Crook, John H.
 1995 Ecology and Culture in the Adaptive Radiation of Tibetan Speaking Peoples in the Himalayas. In *Recent Research on Ladakh 4 & 5*, Henry Osmaston and Philip Denwood, eds. Pp. 19–37. Proceedings of the Fourth and Fifth International Colloquia on Ladakh. London: School of Oriental & African Studies, University of London.
- Crook, John H., and Stamati J. Crook
 1988 Tibetan Polyandry: Problems of Adaptation and Fitness. In *Human Reproductive Behavior*, L. Betzig, M. Borgerhoff Mulder, and P. Turke, eds. Pp. 97–114. Cambridge: Cambridge University Press.
- 1994 Explaining Tibetan Polyandry: Socio-Cultural, Demographic and Biological Perspectives. In *Himalayan Buddhist Villages*, J. H. Crook and H. D. Osmaston, eds. Pp. 735–786. Bristol: University of Bristol.
- Crook, John H., and Tsering Shakya
 1994 Six Families of Leh. In *Himalayan Buddhist Villages*, J. H. Crook and H. D. Osmaston, eds. Pp. 701–734. Bristol: University of Bristol.

- Crow, J. F., and M. Kimura
 1970 *An Introduction to Population Genetics Theory*. New York: Harper and Row.
- Davies, N. B., and I. R. Hartley
 1996 Food Patchiness, Territory Overlap and Social Systems: An Experiment with Dunnocks (*Prunella modularis*). *Journal of Animal Ecology* 65:837–846.
- Dawkins, Richard
 1982 *The Extended Phenotype: The Gene as the Unit of Selection*. San Francisco: W. H. Freeman.
- Durham, William H.
 1991 *Coevolution: Genes, Culture, and Human Diversity*. Stanford: Stanford University Press.
- Foley, Rob A.
 1995 The Adaptive Legacy of Human Evolution: A Search for the Environment of Evolutionary Adaptedness. *Evolutionary Anthropology* 4:194–203.
- Gamble, Clive
 1994 *Timewalkers: The Prehistory of Global Colonization*. Stroud: Alan Sutton.
- Goldstein, Melvyn C.
 1971 Stratification, Polyandry, and Family Structure in Central Tibet. *Southwestern Journal of Anthropology* 27:65–74.
- 1976 Fraternal Polyandry and Fertility in a High Himalayan Valley in Northwest Nepal. *Human Ecology* 4(3):223–233.
- 1977 Population, Social Structure and Strategic Behavior: An Essay on Polyandry, Fertility and Change in Limi Panchayat. *Contributions to Nepalese Studies* 4:47–62.
- 1978 Pahari and Tibetan Polyandry Revisited. *Ethnology* 17:325–337.
- 1981 New Perspectives on Tibetan Fertility and Population Decline. *American Ethnologist* 8:721–738.
- Goldstein, Melvyn C., and Cynthia M. Beall
 1982 Tibetan Fraternal Polyandry and Sociobiology: A Rejoinder to Abernethy and Fernandez. *American Anthropologist* 84:898–901.
- Goody, Jack
 1976 *Production and Reproduction: A Comparative Study of the Domestic Domain*. Cambridge: Cambridge University Press.
- Grafen, Alan
 1984 Natural Selection, Kin Selection and Group Selection. In *Behavioural Ecology: An Evolutionary Approach*, J. R. Krebs and N. B. Davies, eds. Pp. 62–84. Sunderland, Massachusetts: Sinauer Associates.
- Haldane, J. B. S.
 1956 The Argument from Animals to Man: An Examination of Its Validity for Anthropology. *Journal of the Royal Anthropological Institute* 86:1–14.
- Hamilton, William D.
 1963 The Evolution of Altruistic Behaviour. *American Naturalist* 97:354–356.
- 1975 Innate Social Aptitudes of Man: An Approach from Evolutionary Genetics. In *Biosocial Anthropology*, R. Fox, ed. Pp. 133–155. London: Malaby.

- Hiatt, L. R.
1980 Polyandry in Sri Lanka: A Test Case for Parental Investment Theory. *Man* (n.s.) 15:583-602.
- Irons, William G.
1979 Natural Selection, Adaptation, and Human Social Behavior. In *Evolutionary Biology and Human Social Behavior*, N. Chagnon and W. Irons, eds. Pp. 4-39. North Scituate, Massachusetts: Duxbury Press.
1990 Let's Make Our Perspective Broader Rather Than Narrower: A Comment on Turke's "Which Humans Behave Adaptively, and Why Does It Matter?" and on the So-Called DA-DP Debate. *Ethology and Sociobiology* 11:361-374.
1998 Adaptively Relevant Environments and the Study of Human Adaptation. *Evolutionary Anthropology*, in press.
- Kaplan, Hillard S., Jane B. Lancaster, John A. Bock, and S. E. Johnson
1995 Fertility and Fitness among Albuquerque Men: A Competitive Labour Market Theory. In *Human Reproductive Decisions: Biological and Social Perspectives*, R. I. M. Dunbar, ed. Pp. 96-136. London: St. Martin's Press.
- Kelly, Robert L.
1995 *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways*. Washington, D.C.: Smithsonian Institution Press.
- Kitcher, Philip
1985 *Vaulting Ambition: Sociobiology and the Quest for Human Nature*. Cambridge, Massachusetts: MIT Press.
- Levine, Nancy E.
1988 *The Dynamics of Polyandry: Kinship, Domesticity, and Population on the Tibetan Border*. Chicago: University of Chicago Press.
- Levine, Nancy E., and Walter H. Sangree
1980 Conclusion: Asian and African Systems of Polyandry. *Journal of Comparative Family Studies* 11:385-410.
- Levine, Nancy E., and Joan B. Silk
1997 Why Polyandry Fails: Sources of Instability in Polyandrous Marriages. *Current Anthropology* 38:375-398.
- Potts, Rick
1996 *Humanity's Descent: The Consequences of Ecological Instability*. New York: Avon.
- Rogers, Alan R.
1990 The Evolutionary Economics of Human Reproduction. *Ethology and Sociobiology* 11:479-495.
- Schuler, Sidney Ruth
1987 *The Other Side of Polyandry: Property, Stratification, and Nonmarriage in the Nepal Himalayas*. Boulder: Westview Press.
- Sherman, Paul W., and Hudson K. Reeve
1996 Forward and Backward: Alternative Approaches to Studying Human Social Evolution. In *Evolution and Human Behavior: A Critical Reader*, Laura M. Betzig, ed. Pp. 147-158. Oxford: Oxford University Press.
- Smith, Eric Alden
1983 Anthropological Applications of Optimal Foraging Theory: A Critical Review. *Current Anthropology* 24:625-651.

- 1985 Inuit Foraging Groups: Some Simple Models Incorporating Conflicts of Interest, Relatedness, and Central-Place Sharing. *Ethology and Sociobiology* 6:27-47.
- Symons, Donald
1989 A Critique of Darwinian Anthropology. *Ethology and Sociobiology* 10:131-144.
1990 Adaptiveness and Adaptation. *Ethology and Sociobiology* 11:427-444.
1992 On the Use and Misuse of Darwinism in the Study of Human Behavior. In *The Adapted Mind; Evolutionary Psychology and the Generation of Culture*, J. H. Barkow, L. Cosmides, and J. Tooby, eds. Pp. 137-159. Oxford: Oxford University Press.
- Thomas, Nicholas
1989 Domestic Structures and Polyandry in the Marquesas Islands. In *Family and Gender in the Pacific: Domestic Contradictions and the Colonial Impact*, Margaret Jolly and Martha Macintyre, eds. Pp. 65-83. Cambridge: Cambridge University Press.
- Tooby, John, and Leda Cosmides
1990 The Past Explains the Present: Emotional Adaptations and the Structure of Ancestral Environments. *Ethology and Sociobiology* 11:375-424.
1992 The Psychological Foundation of Culture. In *The Adapted Mind: Evolutionary Psychology and the Generation of Culture*, J. H. Barkow, L. Cosmides, and J. Tooby, eds. Pp. 19-136. Oxford: Oxford University Press.
- Tooby, John, and Irven DeVore
1987 The Reconstruction of Hominid Behavioral Evolution Through Strategic Modeling. In *The Evolution of Human Behavior: Primate Models*, Warren G. Kinzey, ed. Pp. 183-237. Albany: SUNY Press.
- Turke, Paul W.
1990 Which Humans Behave Adaptively, and Why Does It Matter? *Ethology and Sociobiology* 11:305-339.
- Werren, John H., and H. Ronald Pulliam
1981 An Intergenerational Model of the Cultural Evolution of Helping Behavior. *Human Ecology* 9:465-483.
- Whittingham, L. A., P. O. Dunn, and R. D. Magrath
1997 Relatedness, Polyandry and Extra-Group Paternity in the Cooperatively-Breeding White-Browed Scrubwren (*Sericornis frontalis*). *Behavioral Ecology and Sociobiology* 40:261-270.